LETTER

Climate change, genotypic diversity and gene flow in reef-building corals

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Abstract

In the ocean, large-scale dispersal and replenishment by larvae is a key process underlying biological changes associated with global warming. On tropical reefs, coral bleaching, degradation of habitat and declining adult stocks are also likely to change contemporary patterns of dispersal and gene flow and may lead to range contractions or expansions. On the Great Barrier Reef, where adjacent reefs form a highly interconnected system, we use allozyme surveys of *c.* 3000 coral colonies to show that populations are genetically diverse, and rates of gene flow for a suite of five species range from modest to high among reefs up to 1200 km apart. In contrast, 700 km further south on Lord Howe Island, genetic diversity is markedly lower and populations are genetically isolated. The virtual absence of long-distance dispersal of corals to geographically isolated, oceanic reefs renders them extremely vulnerable to global warming, even where local threats are minimal.

Tropical coral reefs are increasingly threatened by shifts in the world's climate, overfishing and declining water quality (Knowlton 2001; Wilkinson 2002; Hughes *et al.* 2003). High levels of genetic diversity within populations of corals are likely to be an important element in evolutionary responses to climate change. Populations at high latitudes may be more vulnerable to climate change because they are typically at the margins of geographical ranges, and are likely to be small and isolated (Hughes *et al.* 2002a). However, almost nothing is known about larval connections along latitudinal or thermal gradients, or the relative genotypic diversity of tropical vs. high-latitude coral populations. Here we exploit the vast north–south extent of Australia's Great Barrier Reef (GBR) (10–23°S), and the presence of reefs 700 km further south, at Lord Howe Island (LHI) (31°S; Fig. 1), to examine these issues for the first time. The geographical ranges of approximately one-third of the corals on the GBR extend as far as LHI, the southernmost reef in the Pacific. Dispersal to LHI requires the transport of planktonic larvae via the south-flowing East Australia Current (Wolanski 1994).
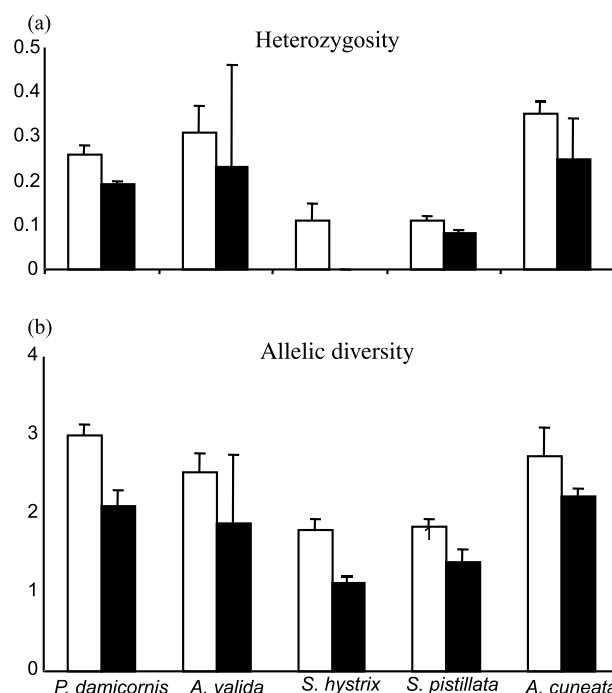
METHODS

To measure genetic diversity and estimate gene flow we made collections of branch fragments from *c.* 3000 corals from three sites at each of the four regional locations (Fig. 1). We chose five common and widespread species with a range of morphologies and life histories, whose ranges extend southwards from the GBR to LHI. One is a broadcast spawner (*Acropora valida*), three are brooders with internal fertilization (*Seriatopora hystrix*, *Stylophora pistillata* and *Acropora cuneata*) and one is a brooder of asexually generated planulae that may also broadcast spawn (*Pocillopora damicornis*; Harrison & Wallace 1990). We sampled reef crests only, to eliminate effects of depth or habitat. Each of the three local sites were separated by 1–5 km. At each site, we collected branch fragments from *c.* 50 colonies/species, within an area <1000 m². We avoided collecting from adjacent colonies that may have formed asexually through recent injury. We determined the genotype of each colony for each of the 4–7 variable allozyme loci as described by Ayre & Hughes 2000. Allele frequencies for the GBR collections are presented in Ayre & Hughes (2000). We estimated the magnitude of

Figure 1 Map of eastern Australia showing four regional locations, separated by up to 2460 km and 17° of latitude, where coral populations were sampled (at three local sites per location) to estimate genetic diversity and gene flow.

Figure 2 (a) Expected heterozygosity and (b) allelic diversity (mean number of alleles per locus) for five coral species, on the Great Barrier Reef (□) and on the high latitude reefs of Lord Howe Island (■). Error bars indicate variation (1SE) among sites.

genetic differentiation using pairwise estimates of F_{ST} (Weir & Cockerham 1984), based on allele frequencies for individual sites or for pooled sites within locations. Local and regional $N_e m$ values were estimated assuming that our sampled populations are in a migration/drift equilibria under an island model (Wright 1969). We applied the Island Model because it is commonly used and permits direct comparison with a range of other studies (Bohonak 1999). Although precise estimates of gene flow are problematic (Whitlock & McCaughley 1999), a recent meta-analysis has confirmed that F_{ST} estimates are powerful predictors of the dispersal capabilities of a range of marine taxa, and for most systems, levels of gene flow should be inversely proportional to F_{ST} (Bohonak 1999). Allele frequencies for the highly clonal *A. valida* were calculated by treating all colonies within each site with identical multi-locus genotypes as single individuals. Diversity was expressed as allelic richness (the number of alleles per locus) and as expected heterozygosity [Nei's (1978) unbiased measure, H_e]. ANCOVA was used to test for evidence of consistent variation with latitude for each of the diversity variables by using distance from Lizard Island as the covariate and species as the main effect. Analyses were performed either using data from the nine GBR sites (Fig. 2) or all 12 GBR and LHI sites.

We chose to use allozyme rather than DNA markers for two reasons. Primarily, obtaining microsatellite primers and informative mtDNA markers has proved to be very difficult for many species of corals. Amplification techniques (e.g. amplified fragment length polymorphism) are vulnerable to contamination by DNA from symbiotic zooxanthellae. For brooding species in particular, where zooxanthellae are present throughout the lifecycle, they are as yet no reliable DNA-based techniques. Four of the five species we used are brooders, which are frequently the dominant species on isolated, oceanic islands. Secondly, allozymes are relatively cheaper and faster, allowing us to cost-effectively sample a suite of species at an unprecedented spatial scale. A disadvantage of allozymes (and of some DNA markers) is the potential for natural selection. Crucially, selection would be expected to affect only a subset of loci, and operate in different directions depending on species and location. In this study, however, our comparison of the GBR and an isolated reef show highly consistent patterns across loci, species and replicate sites that cannot simply be attributable to selection. When DNA techniques improve and become more affordable, we are confident that they will confirm the major results of our study, i.e. most corals show high levels of genetic subdivision, high latitude reefs are genetically depauperate, and levels of gene flow among coral populations separated by a few 100 km of open water are generally very low.

RESULTS

Our data provide unequivocal evidence of regional genetic differentiation, with markedly lower levels of genetic variation on the isolated LHI for all five species (Fig. 2). In contrast, we found no evidence of a latitudinal gradient of genetic diversity in corals within the 1700 km long GBR 'stepping stone' system of reefs. For all three measures of diversity (see Methods), we detected significant changes with latitude only when we included LHI in our analysis ($P < 0.0005$ for all locations, $P > 0.05$ for the GBR only). LHI populations not only display fewer alleles and fewer polymorphic loci (Fig. 2) but they also display very different allele frequencies compared with the GBR, as reflected in our estimates of limited gene flow (Fig. 3). The low genetic diversity and changes in allele frequencies at LHI are best illustrated by the brooding coral *S. hystrix*, which shows no genetic variation at five of six loci that were always polymorphic on the GBR (Fig. 2).

The significantly lower genetic diversity within species at the LHI (Fig 2) is almost certainly because of their extreme isolation and small effective population sizes (N_e) of these high latitude reefs. Populations with low N_e experience loss of alleles through genetic drift (Benzie 1999, 2000; Frankham *et al.* 2002) and N_e may be further depressed by fluctuations in abundance (Hughes *et al.* 1992; Kalinowski & Waples 2002) (which are likely to be more extreme than near range centres), and as a consequence of their complex life histories. In particular, hermaphroditic corals in small marginal populations may show increased reliance on self-fertilization and asexual reproduction. However, we found limited evidence of clonal recruitment for most species with the majority of the 3000 individuals displaying distinct multi-locus genotypes. (The exception was branching *A. valida* which was highly clonal at some sites on both the GBR and LHI.)

We found strikingly high levels of genetic differentiation between GBR and LHI populations for each of the species surveyed (Table 1). Pairwise F_{ST} comparisons for LHI and the GBR were very high (mean ± SE): $F_{ST} = 0.20 \pm 0.02$, consistent with marked variation in gene frequencies, and the lower genetic diversity at higher latitude sites; Fig. 2). (One anomalous exception for *S. hystrix* arises because the dominant genotype at depauperate LHI displays the alleles that are most common at Lizard Island.) On the GBR, our estimates of genetic differentiation within and among regions for these same five species yielded three key results.
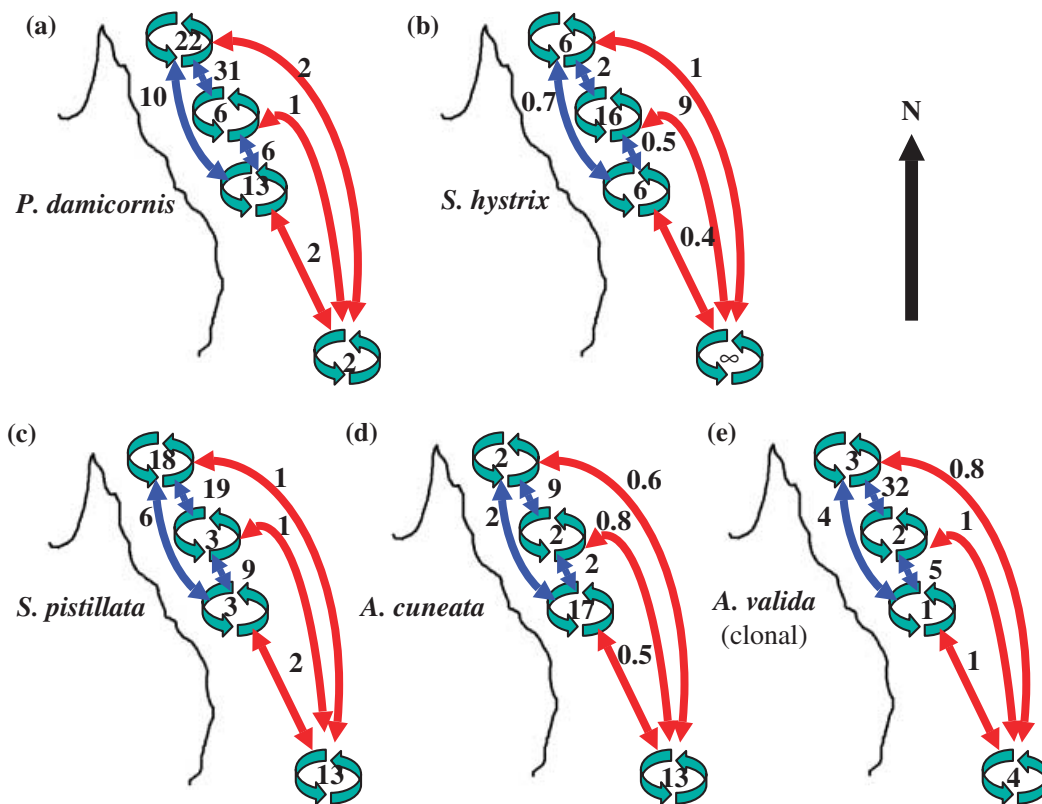
Figure 3 Estimates of gene flow (N_em) for each of five coral species at two scales: among local sites (green arrows) and among regional locations along the Great Barrier Reef (blue arrows) and south to isolated Lord Howe Island (red arrows). Note that for *Seriatopora hystrix* the estimate of $N_em = \infty$ among sites at Lord Howe Island is artefactual and reflect the extraordinarily low allelic diversity at these sites.

Table 1 Pairwise F_{ST} values for comparisons among three sites* within each of three locations on Australia's Great Barrier Reef and the isolated Lord Howe Island (mean ± SE), and among all locations. Among location values treat all sites at each location as a single population. Sample sizes ranged from 37 to 50 per site

Comparison	*Acropora cuneata*	*Acropora valida*	*Pocillopora damicornis*	*Seriatopora hystrix*	*Styllophora pistillata*
Within locations					
Lizard Island	0.136 ± 0.026	0.086 ± 0.056	0.011 ± 0.006	0.042 ± 0.004	0.014 ± 0.009
Davies Reef	0.096 ± 0.050	0.101 ± 0.039	0.040 ± 0.015	0.015 ± 0.008	0.075 ± 0.004
Heron Island	0.015 ± 0.008	0.172 ± 0.063	0.019 ± 0.009	0.039 ± 0.021	0.086 ± 0.045
Lord Howe Island	0.020 ± 0.011	0.058	0.108 ± 0.035	0.000 ± 0.000	0.020 ± 0.01
Among locations within GBR					
Lizard Island–Davies Reef	0.027	0.008	0.008	0.121	0.013
Lizard Island–Heron Island	0.105	0.056	0.024	0.251	0.040
Davies Reef –Heron Island	0.136	0.050	0.040	0.317	0.027
Among GBR and Lord Howe Island locations					
Lizard Island–Lord Howe Island	0.278	0.246	0.137	0.152	0.183
Davies Reef–Lord Howe Island	0.240	0.204	0.176	0.026	0.169
Heron Island–Lord Howe Island	0.343	0.187	0.147	0.405	0.094

Acropora valida was collected from only two sites at Lord Howe Island.

First, we detected low to moderate levels of differentiation among locations on the GBR (Fig. 1), with mean $F_{ST} = 0.082 ± 0.024$. Secondly, for each species, levels of genetic differentiation were similar among sites within locations and among locations (<5 km separation, mean $F_{ST} = 0.063 ± 0.013$ vs. $0.082 ± 0.024$; Table 1). Thirdly, we found consistently lower levels of genetic variation between northern and central regions than central and southern locations (mean $F_{ST} = 0.035$ vs. 0.114, Table 1). The smaller regional-scale differentiation between the northern and central GBR (Table 1) may simply reflect a historical legacy of high rates of gene flow in the geological past (Benzie 1999). However, this result is consistent with contemporary latitudinal attenuation in rates of recruitment by brooded corals (Hughes *et al*. 2002b) and may reflect a greater annual production of larvae in the northern GBR (Kojis 1986).

Based on these levels of genetic differentiation, we estimate that there is almost no gene flow between the GBR and LHI for any of the five species (mean $N_em = 1.1 ± 0.1$, ignoring one outlier for *S. hystrix*; Fig. 3). In contrast, locations up to 1200 km apart on the GBR appear much more highly connected with $N_em = 9.2 ± 2.6$. Our estimates of gene flow among sites within the three GBR locations are similar ($N_em = 8.0 ± 1.8$). (Note however that the effective population sizes at local and regional scales will be vastly different.) The levels of gene flow inferred here for corals fall near the lower range estimated along the GBR for several fishes, giant clams and echinoderms (Benzie 1999), and are similar to a report of low connectivity between GBR and LHI for populations of crown-of-thorns starfish ($N_em = 1.1 ± 0.1$ for corals vs. $1.6 ± 0.5$ for starfish) (Benzie 2000).

DISCUSSION

Our analysis demonstrates that genetic differentiation between regions (and inferred gene flow) varies markedly among coral species. At one extreme, *S. hystrix* is characterized by low gene flow at all scales: among regions, more locally among sites within regions (Fig. 3) and even among habitats (Ayre & Dufty 1994). The low genetic diversity of this species at LHI suggests that all 150 colonies that we sampled there are derived from a very few and perhaps even a single, colonist. Yet, despite very low rates of gene flow, *S. hystrix* has an enormous geographical range, extending northwards from LHI to Japan, east to French Polynesia and west to Africa and the Red Sea (Veron 2000). Although *S. hystrix* must be an effective colonist over geological time frames, our data indicate that of the species we examined, its populations are the most subdivided and the most susceptible to loss of alleles through genetic drift or founder events. Although *Styllophora pistillata* has an equally huge geographical range (Veron 2000), it falls at the opposite end of the spectrum of F_{ST} values that we recorded (Table 1). This disparity indicates that rates of gene flow are not a reliable predictor of the geographical range of corals. Furthermore there is no consistent difference in larval type (brooder or spawner) in pandemic vs. endemic species of corals (Hughes *et al*. 2002a). We conclude that the common but untested assumption that larval duration can explain geographical range (Mora *et al*. 2003) requires much more rigorous assessment. A highly subdivided pandemic, such as *S. hystrix* may be just as vulnerable to climate change as an endemic, especially if the endemic species has higher levels of connectivity among subpopulations throughout its more limited range.

Our results clearly show that corals do not conform simply to Wright's Island Model of gene flow (Wright 1969). Instead, we show that expanses of open-ocean separating Lord Howe and the GBR or between other isolated reefs are far more effective barriers to dispersal than similar distances within continuous reef systems. Presumably, the relatively high estimates of gene flow within the GBR involves a multi-generational sequence of 'steps'.

Even within the high tropics, local populations within the GBR appear to be 'self-seeding'. Estimated rates of gene flow ($N_e m$) between adjacent sites <5 km apart were only slightly lower than rates among distant regions (Fig. 3), although N_e is orders of magnitude lower at the smaller, local scale. Consequently, while long-distance gene flow over multiple generations is sufficient to limit genetic differentiation along the length of the GBR, most recruitment by corals on ecological time frames is decidedly local. In support of this conclusion, hydrodynamic modelling studies indicate that coral larvae can often remain on or near their natal reef for several days, long enough for them to mature and settle locally (Black et al. 1991). Similarly, the scale of stock–recruitment relationships for acroporid corals on the GBR is surprisingly small: recruitment to reefs is strongly correlated with local larval production (Hughes et al. 2001), providing further support for limited dispersal.

Our results have profound implications for the conservation and management of coral reefs in the face of climate change (Hughes et al. 2003). Long-distance dispersal by corals to geographically isolated reefs cannot be achieved incrementally and is likely to be very rare. Consequently, we predict that localized extinctions of isolated populations (e.g. because of oil spills or thermally induced bleaching) will have persistent impacts over very long periods. Furthermore, the limited allelic variation within isolated populations means that they are likely to have a limited capacity to respond to environmental change. The low genetic diversity of corals at Lord Howe Island could be because of its high latitude, isolation from distant sources of larvae or a combination of both. Importantly, we found no latitudinal variation along the length of the highly interconnected GBR, a 1700 km distance that corresponds to a 4–5 °C thermal gradient (Ayre & Hughes 2000). We predict therefore, that when our regional scale approach is replicated elsewhere, it will reveal similar levels of genetic isolation on oceanic reefs closer to the equator.

Finally, both the GBR and LHI are marine reserves, protecting them against local-scale disturbances such as overfishing. However, these two world heritage areas are too far apart to form an interconnecting network, at least for corals, the major habitat-forming species. Consequently, if LHI loses most of its corals to regional or global scale disturbances they are unlikely to be replaced by a significant influx of warm-adapted coral genotypes from the north. MPAs work well as a conservation tool for networks of locations that are close together, relative to the dispersal distance of larvae (Palumbi 2003). While MPAs on isolated reefs may afford significant protection from localized threats such as overfishing, they provide little insurance against loss of local brood stock caused by larger scale disturbances (e.g. coral bleaching because of climate change).

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